Effects of Flow and Seston Availability on Scope for Growth of Benthic Suspension-Feeding Invertebrates from the Gulf of Maine

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Abstract. *Metridium senile*, the frilled sea anemone, and *Modiolus modiolus*, the northern horse mussel, are important members of benthic suspension-feeding assemblages at several rocky hard-bottom subtidal (30–35 m) sites in the Gulf of Maine. Measurements of food availability, rates of food capture, absorption efficiencies, and standard metabolic costs show that inshore populations of *Metridium senile* have a significantly lower scope for growth than offshore populations, despite higher mean concentrations of particulate organic matter inshore. Similar measurements and calculations for *Modiolus modiolus* reveal the opposite pattern. These differences persisted at both of these sites during two summers, 1989 and 1990, when differences in mean temperature were not physiologically significant. Thus temperature is precluded as the primary effect on metabolism and growth. We suggest that these physiological differences reflect a response to flow regime and food availability that appears to be manifested differently for *Metridium senile* and for *Modiolus modiolus*, a passive and an active suspension feeder, respectively. Results from a reciprocal transplant experiment, to measure growth rates, carried out over a one-year period support the calculated scope for growth during the season when maximum growth rates would be expected. The flux of seston appears to be an important factor affecting the organismal performance of the passive suspension feeder (*M. senile*), whereas the concentration of seston is more important for the active suspension feeder (*M. modiolus*).

Introduction

Throughout the rocky subtidal region of the Gulf of Maine (GOM), sessile suspension-feeding invertebrates are a dominant feature of benthic communities (Witman and Cooper, 1983; Sebens, 1985; Witman, 1985; Sebens, 1986; Witman, 1987; Ojeda and Dearborn, 1989). Within the GOM, the abundance of passive and active suspension-feeding invertebrates at a depth of 30–45 m coincides with the occurrence of a particulate maximum layer (PML) (Witman and Sebens, 1988; Townsend and Cammen, 1985), and includes a subsurface chlorophyll maximum (Townsend *et al.*, 1984; Morrison and Townsend, 1988).

Levels of phytoplankton biomass and productivity are higher in the coastal waters of the GOM than in the central open waters (Yentsch *et al.*, 1979; Yentsch and Garfield, 1981). Such regional differences in productivity could affect the dynamics of benthic suspension-feeding communities because of the linkage between the food resources of these communities and the hydrographic events occurring in the overlying water column. These hydrographic events do affect the production and transport of particulate food to the benthos (Graf *et al.*, 1982, 1983; Fréchette and Bourget, 1985a). Benthic-pelagic coupling has been demonstrated for intertidal (Fréchette and Bourget, 1985a) and deep-sea (Graf, 1989) secondary productivity and for successful settlement (Thresher *et al.*, 1989) or recruitment (Townsend and Cammen, 1988) of temperate marine fishes. Regional differences in the quantity of available seston occur between coastal and offshore waters of California where the scope for growth and the shell growth of mussels (*Mytilus edulis*) is food

limited offshore (Page and Ricard, 1990). The biomass and growth rates of suspension-feeding invertebrates depend on the quality (nitrogen content relative to carbon) as well as the quantity of seston (Stuart and Klumpp, 1984; Seiderer and Newell, 1985; Fielding and Davis, 1989; Page and Ricard, 1990; Grant and Crawford, 1991).

Food limitation in dense aggregations of suspension feeders on coral reefs (Glynn, 1973), in cryptic reef habitats (Buss and Jackson, 1981), and among intertidal and infaunal bivalves (Fréchette and Bourget, 1985b; Peterson and Black, 1987) supports the notion that particulate food resources and the distribution and abundance of benthic suspension feeders are related. Food availability is also coupled to current velocity, which ultimately determines the flux of material that can be captured and utilized (Sebens, 1984; Genin *et al.*, 1986). Variability in the near-bottom flow regime also affects the distribution and abundance of benthic suspension feeders through its influence on prey capture (Best, 1988; Patterson, 1991a, b), growth (Shick *et al.*, 1979; Sebens, 1981, 1984), metabolism (Patterson and Sebens, 1989), mode of reproduction and clonal structure of populations (Shick *et al.*, 1979), larval recruitment (Butman, 1986; Genin *et al.*, 1986), and dislodgment from the substratum (Witman, 1987).

We have examined, in two distinct sites, the effects of food availability and water flow on the physiological ecology of two members of a benthic suspension-feeding community. The two sites represent inshore and offshore oceanographic regimes in the GOM. The inshore site—Gull Rock Ledge (GRL), Monhegan Island—and the offshore site—Ammen Rock Pinnacle (ARP), Cashes Ledge—are being used to study the long-term dynamics of benthic communities at 30–35 m. Five-year records of bottom temperatures at these sites show remarkably similar seasonal temperature profiles (Witman, unpub.), which largely eliminates temperature-related effects on metabolism and secondary productivity as the primary determinants of the distribution and abundance of these communities. These two sites are, however, significantly different in annual new production (Townsend and Spinrad, 1986; Morrison and Townsend, 1988) and mean current velocities (Witman, unpub., Table 1).

Metridium senile, the frilled anemone, and *Modiolus modiolus,* the horse mussel, are important components of both the inshore and offshore rocky hard-bottom benthic communities (Witman and Sebens, 1988, 1990; Witman, unpub.). But the two species have different modes of suspension feeding and use different food resources. *Metridium senile* is a passive suspension feeder, while *M. modiolus* is an active suspension feeder; *M. senile* feeds primarily on crustacean and larval zooplankton (Sebens and Koehl, 1984), and *M. modiolus* feeds primarily on phytoplankton (Griffiths and Griffiths, 1987); yet both species can digest detritus (Seiderer and Newell,

1985; Zamer *et al.*, 1987). Although their distribution and abundance on subtidal hard bottoms is patchy, anemones and mussels have very different patterns of density at each site. *Modiolus modiolus* has higher densities at GRL than at ARP, whereas *M. senile* shows the opposite pattern, with higher mean densities at ARP than at GRL (Witman and Sebens, 1988; Witman, unpub.).

We hoped to discern the relative importance of particle flux *versus* seston concentration on scope for growth (SFG) of these two suspension feeders. Although competition for space or food has been invoked as a factor limiting the growth and survival of benthic suspension feeders (Buss and Jackson, 1981; Fréchette and Lefaivre, 1990), the plasticity in the physiological response of a species to different environments influences its growth and survival (Bayne and Widdows, 1978; MacDonald and Thompson, 1986; Zamer and Shick, 1987). Rather than measuring growth directly, the energy available for growth can be determined from an energy budget and used to infer long-term patterns of growth. SFG has provided a quantitative basis for comparing the bioenergetics of bivalve molluscs (Bayne and Widdows, 1978; Wilbur and Hilbish, 1989; Clarke and Griffiths, 1990; Grant and Cranford, 1991) and sea anemones (Zamer and Shick, 1987) exposed to different physical environments and food regimes. Such bioenergetic data should complement direct measurements of growth for benthic species occurring either onshore or offshore in the GOM. Here we report both long-term growth and physiological measurements for *Metridium senile* and *Modiolus modiolus.* These data reflect a response to flow regime and food availability that appears to be manifested differently in the two species.

Materials and Methods

Collection sites and experimental animals

Metridium senile and *Modiolus modiolus* were collected from 30–35 m depth at a coastal site, Gull Rock Ledge, Monhegan Island (43° 45.0′ N, 69° 17.5′ W), and an offshore site, Ammen Rock Pinnacle, Cashes Ledge (42° 51.25′ N, 68° 57.11′ W) in the GOM (Fig. 1). Mixed-gas scuba (NOAA Nitrox I and II) was used in June 1989 for work on *Metridium senile* and in August 1990 for work on *Modiolus modiolus.* Additional information was collected during these periods as described below, and in both years data collection from both sites was completed within one week of each other.

Seston flux and quality

The fluxes of total particulate matter (PM) and particulate organic matter (POM) at the level of the suspension-feeding community (10–20 cm off the bottom) were measured as follows. Scuba divers collected samples of sea-
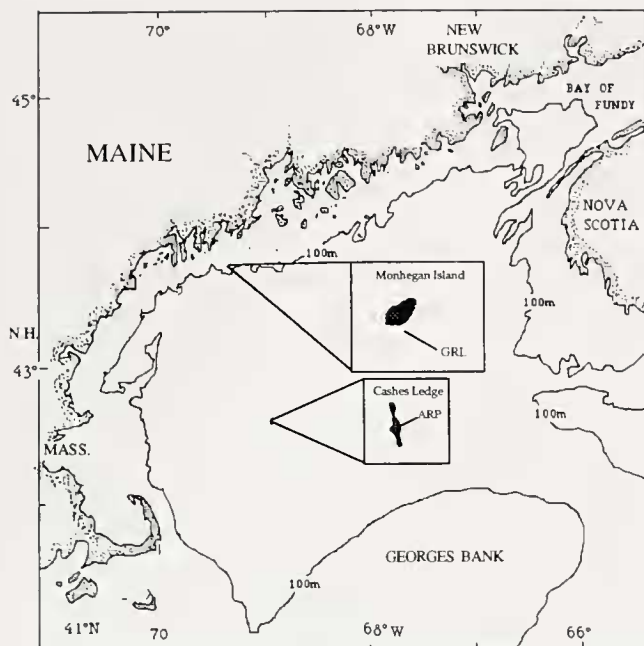
Figure 1. Map of the Gulf of Maine showing the location of the two sites—Gull Rock Ledge just off Monhegan Island and Ammen Rock Pinnacle on Cashes Ledge—where *Metridium senile* and *Modiolus modiolus* were collected. Dotted line represents 100-m depth contour.

water in 5-liter horizontal Niskin bottles. The divers held the bottles with one opening facing upstream into the ambient current. While remaining neutrally buoyant to avoid any resuspension of particulate matter from the benthos, they then triggered the bottles from the downstream side. Horizontal current velocity (cm s^{-1}) was measured simultaneously with electromagnetic current meters (InterOcean model S4) at the same location and time that the samples were collected. The recorded flow speeds were the averages of measurements of 1- to 5-min duration at 2 Hz (120 data points min^{-1}). The horizontal flux of particulate food moving past the suspension-feeding community was calculated as flux = velocity × POM (μg POM cm^{-2} s^{-1}). Replicate 0.5-l samples ($N = 10$) of benthic water from each site were filtered onto preweighed and baked (450°C) GF/F filters, frozen (-20°C), and returned to Bigelow Laboratory for Ocean Sciences for a determination of ash-free dry weight (AFDW = organic content) and carbon, hydrogen, and nitrogen (CHN) content. Filters for the calculation of PM and POM were washed with isotonic ammonium formate to remove salts. PM filters were then dried at 60°C for 24 h and weighed. Filters used for measuring POM were weighed and then combusted at 450°C for 6 h, and AFDW was calculated by difference. Filters for CHN analysis were kept under desiccation until just before analysis, and then freeze-dried again. Samples were combusted in a Control Equipment Corporation (Perkin Elmer) 240 XA elemental analyzer

with an automatic sampler in an air-tight box to keep the samples dry, and acetanilide was used as a standard. No desiccation was provided while the samples were being processed. The values for particulate food fluxes, concentration of seston, and seston C:N ratios obtained at the two sites, GRL and ARP, were statistically compared with a Student's *t* test on arcsine or log-transformed data.

Biochemical composition of benthic invertebrates

Whole freeze-dried anemones and mussels ($N = 5–7$) were pulverized, and the powder from each individual anemone or mussel was subsequently subsampled in triplicate. The subsamples were each processed as described above to minimize the rehydration of the tissues. Still another set of samples of freeze-dried anemone and mussel tissues was combusted at 450°C as described above, and a CHN analysis was run on the remaining ash (= inorganic content). The CHN analyses of tissues and ash were used together to determine the proximate biochemical composition of tissues; the stoichiometric equations of Gnaiger and Bitterlich (1984) were applied as described by Zamer and Shick (1989). The tissue C:N ratios and proximate biochemical composition of tissues from animals collected at GRL and ARP were statistically compared with a Student's *t* test on arcsine or log-transformed data.

Scope for growth

The calculation of scope for growth (SFG) entailed the measurement of several parameters, specific for either mussels or anemones. Some of these measurements could not be made in the field. In particular, live anemones from GRL and ARP were returned to Bigelow Laboratory so that the maximum size of the tentacular crown in still water could be determined. This, in turn, allowed us to calculate the tentacular crown areas of individuals used in the measurement of respiration and ammonia flux. The regression of freeze-dried weight (X) on the maximum width of the tentacular crown (Y) (GRL: $Y = 2.44X^{0.332}$, $r^2 = 0.981$, $N = 7$, $P = 0.0001$; ARP: $Y = 2.38X^{0.289}$, $r^2 = 0.969$, $N = 6$, $P = 0.006$) was established for both populations as described for west coast populations of *M. senile* by Sebens (1981), and was used to calculate the maximum area of the tentacular crown.

These same anemones were also used to assess the effect of flow on the deformation and subsequent decrease in the size of the tentacular crown. This assessment was made in a recirculating flow tank (Vogel and LaBarbera, 1978) with the aid of close-up photographs, taken from above, of the anemone tentacular crown as it changed morphology under flow speeds up to 20 cm s^{-1}. The percent deformation under a specific flow regime was then applied to values for anemone tentacular crowns at GRL and ARP, allowing us to determine the maximum surface area

available for prey capture. Filtering efficiency of the tentacular crown at different flow speeds was estimated from the model described for the soft-coral *Alcyonium siderium* by Patterson (1991a [Fig. 10], b [Fig. 3]). This model is also applicable to *M. senile* (Patterson, pers. comm.), and describes an inverse relationship between flow speed or Reynolds number and filtering efficiency by comparing the number of particles captured to the total number of particles that passed by the filtering element.

Anemones returned to the laboratory were fed a specific ration of food (*Artemia* sp. nauplii; <5% of anemone wet biomass) known to be in the size range of food captured by these anemones (Sebens and Koehl, 1984) and representative of the zooplankton that are known to make up a major portion of the diets of many carnivorous sea anemones (Shick, 1991), and of *M. senile* in particular (Sebens and Koehl, 1984). The absorption efficiency was determined at the measured temperature of the site, and only on animals that completely ingested the ration. All ejecta were collected with a syringe 24 h after feeding. Extraneous mucus was avoided, but collections of ejecta undoubtedly included mucus within the digested food bolus. The absorption efficiency of material ingested by anemones was determined by the ratio method of Conover (1966). This method assumes that only the organic component is significantly affected by the digestive process and compares changes in the proportion of organic matter in the food and feces. The organic content of food and feces was determined by vacuum filtering samples onto preweighed and combusted GF/F filters, and rinsing with isotonic ammonium formate to remove salts. The filters were then dried at 60°C for 24 h, weighed, and combusted at 450°C for 6 h. The AFDW of the food and feces was then calculated by difference, and the absorption efficiency of organic matter was calculated as described by Conover (1966).

The maximum amount of seston that could be caught by individual anemones at a specific flow speed was calculated as described by Best (1988), where the amount of seston caught is proportional to the volume of water processed (surface area of filter [= tentacular crown] × speed of flow) multiplied by the seston concentration and filtering efficiency. This value is equivalent to total energy consumption (C) in the balanced energy equation (see below), and is multiplied by the absorption efficiency in the calculation of total energy assimilated (A).

Logistic constraints in the field and in the laboratory precluded the measurement of clearance rate and absorption efficiency for *Modiolus modiolus*. But the literature on this mussel contains laboratory (algal monocultures, Winter, 1969, 1978) and field (natural seston, Navarro, 1990; Navarro and Thompson, 1994) measurements of the required values. Navarro (1990) studied *M. modiolus* from Newfoundland, and the mussels from this study had

a smaller range of dry tissue weights (1.5–6.68 g). He observed only a slight, and insignificant, seasonal pattern for changes in clearance rate: those in the spring and summer remained consistently high and were not correlated with changes in temperature. Furthermore, the clearance rates Navarro (1990) calculated for August are not significantly different from our estimates calculated with the allometric equations of Winter (1969, 1978). Because the POM concentrations (0.38 to 1.36 mg l^{-1}; Navarro, 1990) and temperatures experienced by Newfoundland and GOM mussels are very similar, we used the August 1987 allometric equation from Navarro (1990, $Y = 0.91W^{0.53}$) on mussels employed in respiration and ammonia excretion experiments to calculate weight-specific clearance rates for GOM mussels feeding on natural seston. We then used these calculated clearance rates and covariance procedures (described below) to obtain a weighted clearance rate.

During their two-year study, Navarro (1990) and Navarro and Thompson (1994) used four different techniques (ash ratio, silicate ratio, organic carbon, and chloropigments) to measure absorption efficiency. Despite small, but significant, differences between methods (Navarro and Thompson, 1994), none of the four techniques showed significant seasonal variability or any effect of body size on the efficiencies of absorption for natural seston by *M. modiolus*. Both Winter (1978) and Navarro (1990) found that absorption efficiency was independent of body size. We applied the mean value of the pooled absorption efficiencies ($N = 188$, 76.2%) for natural seston for all seasons from Navarro (1990) to our samples at both sites.

The seston samples from GRL and ARP were analyzed for ash-free CHN content, and the percent organic carbon values of the seston were used, with the relationship described by Salonen *et al.* (1976) uncorrected for nitrogen, to calculate the energy content of the POM. The energetic value of the natural seston at the time of the experiments was used to determine the total energy ingested by the anemones and mussels at each site.

Respiration measurements

The respiration rates of anemones and mussels collected from onshore and offshore sites were measured after at least 24 h, and as long as 36 h, without food. Due to equipment shortages, respiration on all anemones could not be measured simultaneously after 24 h without food. A period of starvation was required to avoid, as much as possible, the costs associated with digestion or biosynthesis of macromolecules (*i.e.*, specific dynamic action). Specific dynamic action is very likely a consistent feature of both these suspension feeders in nature but, without any knowledge of their prior feeding history or the degree of specific dynamic action expressed, we chose to measure

respiration and calculate SFG on post-absorptive animals. Data about the return of anemones to pre-prandial rates of respiration are scarce; however, in the case of *Anemonia viridis*, post-prandial rates of respiration were at, or below, pre-prandial rates from 24–36 h after a meal at 10°C (Shick, 1991, Fig. 3.9), while similar changes in *Aiptasia diaphana* were observed 12–24 h after a meal at 24°C (Shick, 1991, Fig. 3.9). Assuming that these symbiotic anemones are exhibiting typical times of returning to pre-prandial respiration rates, the times used here are consistent with those results. Indirect calorimetry was accomplished with oxygen electrodes (Nester Inc., non-oxygen-consuming) in fixed-volume, closed, Plexiglas respirometers at the ambient temperature (6–9°C) and salinity of collection; filtered (1.0 μm) seawater was used.

When *Modiolus modiolus* were collected in 1990, ambient temperatures at the two sites differed by less than 1°C (GRL, 9.2°C; ARP 8.6°C); but in 1989, when *M. senile* were collected, the differences were larger (GRL, 6.2°C; ARP 4.6°C). Therefore, to correct for these temperature effects, calculations of Q_{10} were made and applied to acute measurements, made on site, of respiration (Q_{10} = 1.93), and ammonium excretion (Q_{10} = 2.12) in freshly collected ARP anemones. The same set of anemones was used for measurements of respiration and ammonium excretion at about 4.6°C and 6.2°C. The values obtained were used in the formula $Q_{10} = (R_2/R_1)^{10/T_2 - T_1}$; and the resulting Q_{10} value was used to correct for temperature effects according to the formula: $R_2 = R_1 \cdot Q_{10}^{(T_2 - T_1/10)}$, where R = rate of process and T = temperature.

The unidirectional flows of the seawater within the chambers were relatively similar to *in situ* flows at each site (qualitatively determined by measuring particle speed visually), using a rheostat-controlled motor and a stirring wheel within the Plexiglas chamber. The different flow regimes within these chambers were sufficient to maintain maximum diffusion between the seawater and electrode and, therefore, sensitivity of the electrode to changes in oxygen concentration. The decline in oxygen concentration was begun 15 to 30 min after the animals were placed in the chambers under reduced lighting. Visual observations showed that *Metridium senile* was fully expanded during all respirometry runs, and *Modiolus modiolus* was actively pumping. Oxygen consumption was not measured below 70% of ambient; at this level the rate of uptake in oxyconforming species becomes dependent on external concentrations. Measurements of respiration were made over 1–4 h, depending on individual anemone or mussel biomass.

The oxygen consumption was either monitored continuously with a data logger equipped with an analog-to-digital converter, or manually recorded every 5 min and converted to rates of oxygen consumption (Table II) per individual. Rates were calculated from the slopes of oxygen consumption plotted against time. Blank controls with no animal, run before and after each experiment, were averaged and subtracted from the experimental rates. Rates of oxygen consumption for each animal were compared against its freeze-dried weight of tissue.

Ammonia excretion

Rates of ammonia excretion and respiration were determined at the same time and on the same animals. Seawater samples were taken from the respiration chamber before and after each respiration measurement. These samples were filtered (0.2 μm), frozen, and analyzed according to the phenol-hypochlorite method of Solorzano (1969). Rates of excretion were used with respiration measurements to calculate O:N (oxygen:nitrogen) ratios; that is, the atomic ratio of oxygen consumed and ammonia-nitrogen excreted. The O:N ratio can then be used to estimate the amount of protein catabolized relative to total carbohydrate and lipid, with low O:N ratios indicative of high protein catabolism. O:N ratios have been used as metabolic indicators and can provide information about the physiological state (*i.e.*, respiratory substrate being utilized) of the organism (Mayzaud and Conover, 1988; Szmant *et al.*, 1990).

The energy conversion factors for oxygen (0.45 J per μmol O_2) and ammonia (0.34 J per μmol NH^{4+}) were from Gnaiger (1983) and Elliot and Davison (1975) respectively. The respiration and excretion costs were directly measured on all anemones and mussels used in this study.

In analyzing the physiological measurements reported here, weight-specific rates were not compared. This is because physiological processes, especially respiration, scale allometrically; that is, they generally do not increase isometrically with volume or biomass (Patterson, 1992). Such data therefore violate the assumption of isometry required when measures of biomass are used to normalize the data. We have therefore used an analysis of covariance (ANCOVA) with dry weight as the covariate, and the individual slopes from each site used to weight all measurements within a site to an animal of standard size and tissue dry weight, whether anemone (grand mean = 2.53 g, range of 0.55 to 4.99 g [ARP], 0.58 to 6.22 g [GRL]) or mussel (grand mean = 7.61 g, range of 4.59 to 11.12 g [ARP], 1.67 to 15.24 g [GRL]) (Packard and Boardman, 1988). Regressions of dry weight upon the process of interest, from which the slopes were obtained for weighting purposes, are listed in Table II.

Calculating scope for growth

These weighted physiological responses of anemones and mussels were then converted to energy equivalents and used in the balanced energy equation to calculate

SFG, the energy available for growth and reproduction after maintenance costs are satisfied (Widdows and Johnson, 1988). Scope-for-growth calculations provide a rapid and quantitative method of assessing the physiological, and therefore energetic, status of an animal under different environmental conditions. The balanced energy equation is expressed as

$$C = P + R + U + F$$

where C = total consumption of food energy; P = somatic and gamete production; R = respiratory energy expenses; U = energy lost as waste or excreta; F = fecal energy loss. The absorbed ration, A, is the product of consumption, C, and the efficiency of absorption of energy from the food. Production can then be expressed as

$$P = A - (R + U)$$

and is estimated from the difference between the energy absorbed from food and the energy expenses of respiration and excretion, which is termed the SFG (Widdows and Johnson, 1988). Scope for growth and the individual measurements used to calculate SFG on GRL and ARP populations of *M. senile* and *M. modiolus* were tested statistically with a Student's *t* test at the 0.05 level of probability. SFG was calculated only for individual mussels and anemones for which respiration and ammonia excretion had been directly measured.

A condition index was also calculated for *Modiolus modiolus*; freeze-dried soft-tissue weight and dry shell weight were used to compare metabolism directed at shell with somatic growth, as described by Crosby and Gale [1990; CI = dry soft tissue wt. (g) × 1000/dry shell wt. (g)]. The condition index chosen is essentially a body component index, with higher values indicating energy directed towards tissue growth, and lower values indicating energy directed towards shell growth.

Reciprocal transplants and growth measurements

Metridium senile and *Modiolus modiolus* were transplanted from GRL at 30 m depth to the same depth offshore (ARP), and *vice versa*, in July 1989. The initial collection protocol consisted of removing mussels and anemones from their original habitat, avoiding the collection of anemone clonemates based on color, and measuring their size. For mussels, size was recorded as shell length in centimeters (range of 4.33 to 13.33 cm [ARP], 4.84 to 12.98 cm [GRL]) measured with Vernier calipers. For anemones, size was recorded as displacement volume (range of 3.0 to 55.0 ml [ARP], 2.0 to 50.0 ml [GRL]). For *M. senile*, regressions of volume displacement onto tissue dry weight were established for both sites by collecting anemones, forcing them to fully contract, blotting them dry, and measuring their displaced volume in a 1-l

graduated cylinder filled with seawater. These animals were returned to the laboratory and dried to a constant weight at 60°C.

The transplantation proceeded as follows: Mussels and anemones were placed into one of three numbered compartments of a Vexar cage on a 80-kg base; the base measured 150 × 70 cm. Five replicate compartments were randomly assigned to each treatment and control, with treatments consisting of transplants from coastal to offshore habitats, and transplants from offshore to coastal habitats. Control groups of mussels and anemones were removed and returned to their original habitats in cage compartments. The complete experimental design at one site consisted of 50 replicate mussels and 40 replicate anemones for each treatment and control. Experimental and control animals were collected by scuba in August of 1990, and remeasured as described above. The growth data were analyzed with Ford-Walford plots and ANCOVA techniques. We also measured the total tissue dry weight of all individual *M. modiolus* so we could compare shell growth with somatic tissue growth.

Results

Current velocities, seston concentration, and seston quality

Mean current velocities were almost ninefold higher at ARP than at GRL in 1990 (Table I) and are typical of those from other years (Witman and Sebens, 1988, unpub.). Both PM and POM concentrations were significantly greater (*t* test, $P < 0.05$) at GRL than at ARP in 1989 and 1990 (Table I). When the flow and POM values are used to calculate mean flux of POM at both sites in 1990, we can see that ARP does exhibit higher fluxes of particulate food despite having lower concentrations of POM (Table I). We used current velocities from 1990 to calculate the POM flux at GRL in 1989, assuming that the data for the two years would be similar. This assumption is supported by the consistently lower current velocities observed at GRL and other inshore sites in 1991, 1992, and 1993 (Witman, unpub., Table I). Additionally, using the flow data from subsequent years or the mean of those years does not significantly change the differences in SFG or assimilated energy described below. Seston quality, as determined by the C:N ratio, was not significantly different within each year between sites (Table I). The difference in seston quality between years may reflect the seasonal difference in C:N ratios due to an increase in the detrital component of the seston as nitrogen is removed by zooplankton and bacteria. All C:N ratios suggest that the POM consisted primarily of phytoplankton and bacteria rather than refractory organic material. Although no effort was made to fractionate the seston into its different components, zooplankton will also contribute to

Table I

Average flow speeds and seston quantity and quality for Gull Rock Ledge Island (GRL) and Ammen Rock Pinnacle (ARP) in 1989 and 1990

	1989			1990		
	GRL		ARP	GRL		ARP
Flow[1]	ND		18.3 ± 10.9	2.9 ± 1.7		24.8 ± 12.5
			$(N = 420)$	$(N = 1847)$		$(N = 798)$
PM[2]	2.54 ± 1.41	$P = 0.036$	1.49 ± 0.69	5.54 ± 1.43	$P = 0.001$	2.87 ± 1.86
	$(N = 10)$		$(N = 10)$	$(N = 10)$		$(N = 10)$
POM[3]	0.92 ± 0.51	$P = 0.034$	0.54 ± 0.25	2.0 ± 0.51	$P = 0.001$	1.03 ± 0.67
	$(N = 10)$		$(N = 8)$	$(N = 10)$		$(N = 10)$
Flux[4]	2.67		9.88	5.80		25.54
C:N[5]	3.61 ± 1.09		4.16 ± 1.65	8.39 ± 3.26		6.76 ± 2.11

Flow speeds are 1–5 min averages of measurements of 1–5 min duration at 2 Hz, 120 data points min^{-1}, N = the total number of readings for the specific measurement. Mean flow speeds in 1991 for GRL (3.3 cm s^{-1}), 1992 (5.28 cm s^{-1}), and 1993 (2.64 cm s^{-1}) (Witman, unpub. data). ND = not determined.

[1] cm s^{-1} (mean $\pm$ SD).

[2] Total particulate matter, one-tailed t test (mg l^{-1} [mean $\pm$ SD]).

[3] Particulate organic matter, one-tailed t test (mg AFDW l^{-1} [mean $\pm$ SD]).

[4] μg POM cm^{-2} s^{-1}; 1989 GRL value determined using 1990 flow.

[5] $\mu g/\mu g$ (mean $\pm$ SD, $N = 5$).

the total carbon and nitrogen pools in the seston. Calculated according to the equations of Salonen *et al.* (1976) the energy content (J mg^{-1}) of POM in 1989 was 8.8 for ARP and 7.3 for GRL, while in 1990 the POM values were 13.8 J mg^{-1} for ARP and 15.8 J mg^{-1} for GRL.

Scope for growth

The energetic conversions for the physiological responses and SFG of *Metridium senile* and *Modiolus modiolus* are presented in Figure 2. For most measured or calculated responses, except respiration (R) and energy assimilated (A), anemones from ARP had significantly higher rates when analyzed by ANCOVA (Table II) and weighted to an anemone of standard size (Table II, Fig. 2a). Scope for growth of ARP anemones was also significantly higher than for GRL anemones in June 1989 (Fig. 2a). Measured rates of respiration, and therefore maintenance costs, at ARP were consistently and significantly lower. Assessment of food, and therefore energy, consumption by anemones is complicated by the effects of flow on the flux of food, prey capture area, and capture or filter efficiency. Photographs of the tentacular crown show that for ARP anemones the surface area for prey capture decreased significantly ($P < 0.05$, $N = 5$ for each site on arcsine-transformed data)—to 50% of maximum on average—at the mean current velocity (18.29 cm s^{-1}), but for GRL anemones the prey capture area decreased by only 30% at ambient flows of 3.44 cm s^{-1}. According to the model of Patterson (1991a, b), the filtering efficiency is 40% for ARP anemones and 52% for GRL anemones. The calculated consumption (C) of total particulate matter

(ARP, 13.91 ± 1.85 mg h^{-1}; GRL, 12.87 ± 2.81 mg h^{-1}), and POM (ARP, 5.04 ± 0.67 mg h^{-1}, GRL, 4.66 ± 1.02 mg h^{-1}), when converted to energy equivalents, was significantly different between sites (Fig. 2a, $P = 0.019$), but the total amount of assimilated energy (consumption times absorption efficiency = A) was not significantly different ($P = 0.069$, Fig. 2a), although the mean assimilated energy was higher in ARP anemones. The total particulate or POM rations available to ARP and GRL anemones averaged from 0.3 to 1.1% of the total body weight of anemones from either site. Our weighted estimates of absorption efficiency for ARP and GRL anemones were not significantly different from each other, although the mean absorption efficiency was higher in ARP anemones (Table II). An inverse relationship between the size of daily ration and absorption efficiency has been described for sea anemones (Shick, 1991, see Fig. 2.12 in this ref.). This relationship suggests that by providing *Artemia* sp. in amounts up to 5% of body weight as rations for determining absorption efficiency, we probably underestimated this factor.

Measurements on *Modiolus modiolus* reveal a pattern distinctly different from that exhibited by *Metridium senile*. Mussels from GRL consistently had a higher SFG than mussels from ARP in August 1990, and all components, except for costs associated with waste production (U), of the SFG calculation were significantly higher in GRL anemones (Fig. 2b). There were no significant differences in the weighted clearance rates (Table II) between ARP and GRL. Absorption efficiencies and clearance rates reported for *M. modiolus* in laboratory

A

Metridium senile

B

Modiolus modiolus
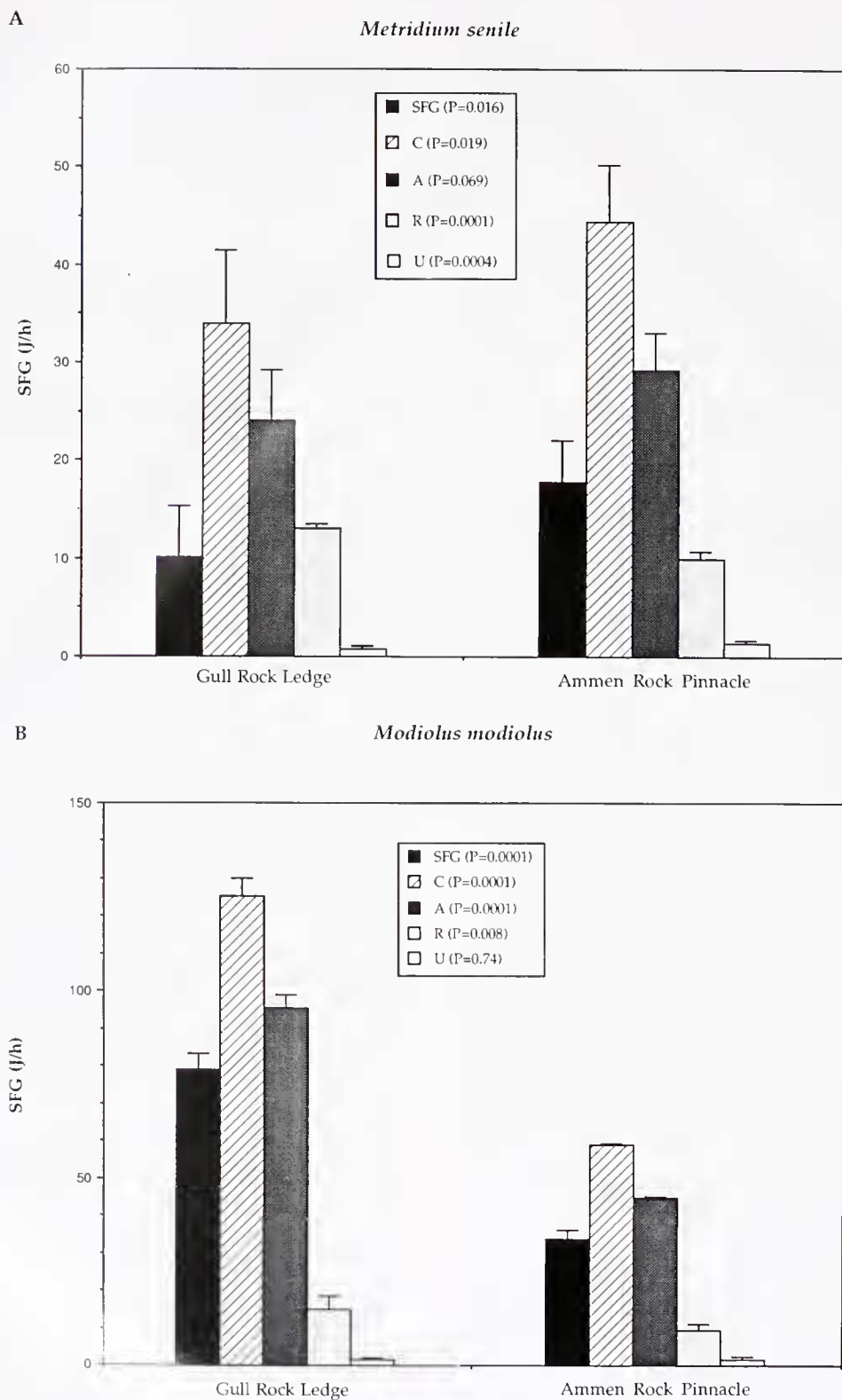
Figure 2. Calculated scope for growth (J h^{-1}) and measured or calculated components used in calculation (mean ± SD). C = total consumption of food energy; A = assimilated energy is the product of total consumption and absorption efficiency; R = respiratory energy costs; U = energy lost as excreta; P = production (or scope for growth). P = A − (R + U). (A) *Metridium senile*. (B) *Modiolus modiolus*. P values are the result of an unpaired, one-tailed *t* test comparing sites.

Table II

Measured and calculated physiological responses for Metridium senile *and* Modiolus modiolus

| Function	Location	N	Rate	P value
Metridium senile				
Absorption efficiency (percentage ± SD)	ARP	6	68 ± 18	P > 0.05
		$(Y = -0.184X - 0.176, N = 6, r^2 = 0.942, P < 0.001)$		
	GRL	7	58 ± 23	
		$(Y = -0.139X - 0.392, N = 6, r^2 = 0.799, P < 0.025)$		
Respiration (μmol O$_2$ h^{-1} ± SD)	ARP	6	22.28 ± 1.51	P = 0.0001
		$(Y = 7.202X + 3.98, N = 6, r^2 = 0.985, P = 0.0001)$		
	GRL	7	29.03 ± 0.86	
		$(Y = 10.81X + 1.80, N = 7, r^2 = 0.999, P 0.0001)$		
Ammonium excretion (μmol NH$_4^+$ h^{-1} ± SD)	ARP	6	7.47 ± 1.72	P = 0.0001
		$(Y = 2.408X + 2.54, N = 6, r^2 = 0.864, P < 0.005)$		
	GRL	7	2.56 ± 1.05	
		$(Y = 2.087X - 1.71, N = 7, r^2 = 0.937, P < 0.001)$		
Modiolus modiolus				
Clearance rate (l h^{-1})	ARP	5	4.2 ± 0.23	P < 0.05
		$(Y = 0.408X + 1.03, N = 5, r^2 = 0.999, P = 0.0001)$		
	GRL	6	3.93 ± 0.5	
		$(Y = 0.406X + 0.91, N = 6, r^2 = 0.996, P = 0.0001)$		
Absorption efficiency (percentage)	ARP	5	76.2 (Navarro, 1990)	
	GRL	6	76.2 (Navarro, 1990)	
Respiration (μmol O$_2$ h^{-1} ± SD)	ARP	5	21.26 ± 3.32	P = 0.041
		$(Y = 4.063X - 9.63, N = 5, r^2 = 0.899, P < 0.01)$		
	GRL	6	33.48 ± 7.47	
		$(Y = 3.652X + 5.71, N = 6, r^2 = 0.869, P < 0.005)$		
Ammonium excretion (μmol NH$_4^+$ h^{-1} ± SD)	ARP	5	4.72 ± 2.42	P > 0.05
		$(Y = 1.658X - 7.90, N = 5, r^2 = 0.740, P < 0.05)$		
	GRL	6	5.08 ± 1.07	
		$(Y = 0.571X + 0.74, N = 6, r^2 = 0.887, P < 0.005)$		

Regression formulas from which slopes were obtained are included. Results are weighted to a standard size anemone (2.53 g) or mussel (7.60 g) using an analysis of covariance (ANCOVA), with dry weight as the covariate, as described by Packard and Boardman (1988). Probability (P) values are from a Student's *t* test.

and field experiments (Winter, 1969, 1978; Navarro, 1990) suggest that these processes are largely invariant between populations. This lack of variation supports our application of literature values to ARP and GRL individuals. The higher SFG values appear to be correlated with differences in POM concentration and subsequent total energy intake for GRL mussels (Table I), rather than with flow regimes or flux of food—although flow itself may have a negative impact on active suspension feeders (see Discussion).

The tissue C:N ratios, the energetic content (*i.e.*, the specific enthalpy of combustion [kJ g^{-1} organic mass]), and the lipid, carbohydrate, or protein fractions from the biochemical composition of *M. modiolus* and *M. senile* were not significantly different ($P > 0.05$) between sites (Fig. 3; Table III). The lipid values for anemones and mussels must, however, be interpreted with caution. Although the samples remained desiccated until just before analysis, they could not be kept under continuous desiccation during the CHN analysis. This

increases the likelihood of hygroscopic absorption of water and a corresponding increase in H content that would lead to higher lipid values. Higher lipid values would also contribute to the energy content of tissues, which for *M. senile* is slightly higher than values reported for other species of anemones (Shick, 1991).

Both the gross and net growth efficiencies (Table III) track with the calculated SFG; net growth efficiencies (K_2), calculated on an energetic basis, are higher in populations of anemones and mussels with higher SFG. The O:N ratio for *M. modiolus* was not significantly different between sites and indicates that protein is the primary catabolic substrate being utilized (O:N ranging from 3 to 16; Mayzaud and Conover, 1988). Although anemones are reported to rely heavily on protein as a catabolic substrate (Shick 1991), the O:N ratios for *M. senile* were significantly different between sites. The ratios indicate that metabolic requirements were fueled primarily by protein at ARP, but that lipid and car-

A

Metridium senile

B
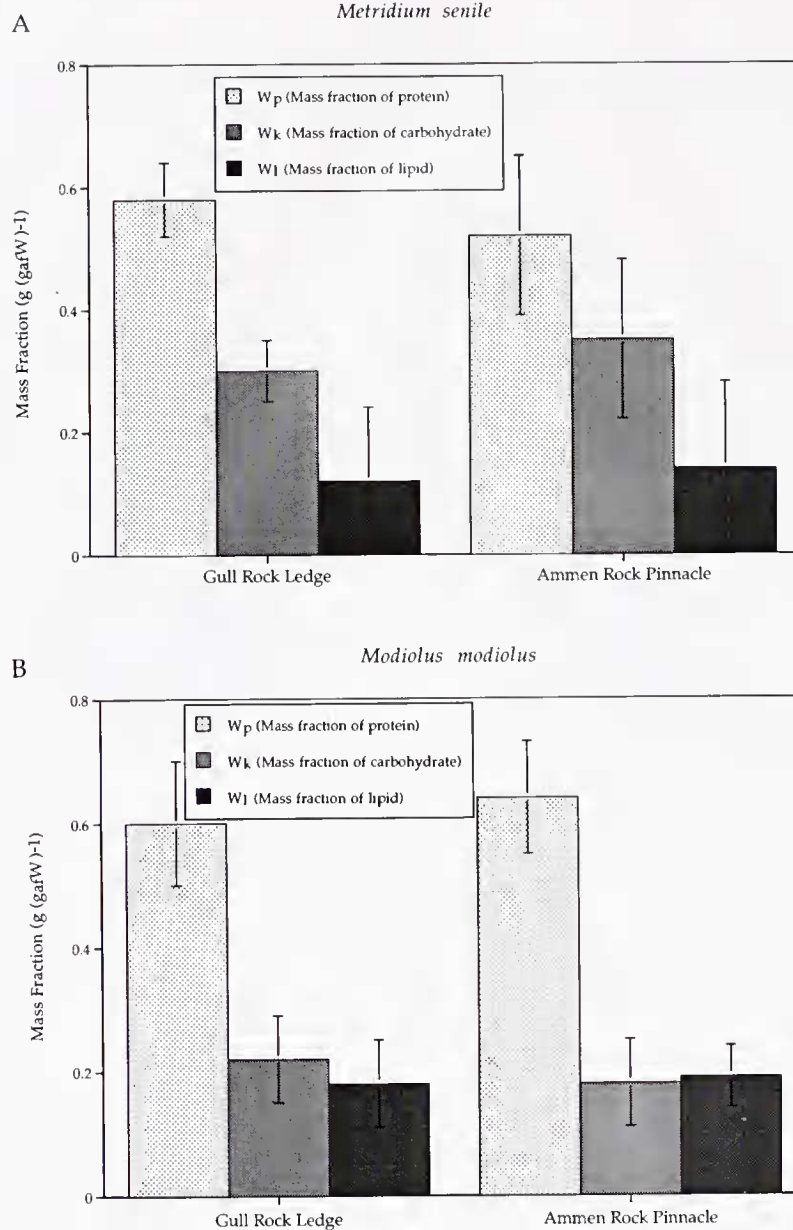
Modiolus modiolus

Figure 3. Proximate biochemical composition of *Metridium senile* (A), and *Modiolus modiolus* (B) for GRL and ARP sites. W_p = mass fraction of protein, W_k = mass fraction of carbohydrate, W_l = mass fraction of lipid. All results are mass fractions g $(g_{af} W)^{-1}$ ± SD as units.

bohydrate were the dominant respiratory substrates at GRL. If GRL anemones were feeding on resources that were enriched in lipid and carbohydrate, or were depending on stored forms of these constituents, this was not reflected in any significant differences in the biochemical composition of anemone tissues between the two sites. Lastly, the values of tissue C:N, seston C:N, and O:N that we observed for anemones and mussels suggest that the supply of nitrogen in the seston was adequate at both sites.

Reciprocal transplants and growth of anemones and mussels

All regressions for the transplant comparisons were significant (ANOVA, $P < 0.05$), with the number of samples for each comparison being the number of individuals recovered (minus losses due to storms and mortality) for which we could match numbered tags with individual identifying marks.

The relationship between volume displacement (Y) and dry tissue weight (X) was significant for samples of *Me-*

Table III

Growth efficiencies and metabolic and condition indices for Metridium senile *and* Modiolus modiolus *collected from onshore (Gull Rock Ledge [GRL]) and offshore (Ammen Rock Pinnacle [ARP]) sites in the Gulf of Maine*

	Metridium senile			Modiolus modiolus		
	GRL	ARP	P value	GRL	ARP	P value
K_1[1]	20 ± 10	39 ± 5	0.0009	63 ± 3	57 ± 4	0.02
K_2[2]	28 ± 15	60 ± 7	0.0004	82 ± 4	75 ± 5	0.02
O:N[3]	38 ± 22	7 ± 5	0.003	14 ± 6	15 ± 5	0.57
CI[4]	NA	NA	NA	146 ± 38	104 ± 32	0.035
C:N[5]	5.39 ± 0.63	6.22 ± 1.34	0.248	5.27 ± 0.88	5.19 ± 0.73	0.255
EC[6]	−23.91 ± 0.73	−23.78 ± 1.22	0.849	−25.26 ± 3.32	−24.38 ± 1.11	0.52

P values based on the results of a Students *t* test (unpaired, one-tailed for growth efficiencies; unpaired, two-tailed for O:N, CI, and EC; percentages, ratios, and indices are not normally distributed and were either arcsine or log transformed before analysis).

[1] Gross growth efficiency (Calculated SFG/Energy Consumed × 100%, mean ± SD; GRL, $N = 7$; ARP, $N = 6$).

[2] Net growth efficiency (Calculated SFG/Energy absorbed × 100%, mean ± SD, GRL, $N = 7$; ARP, $N = 6$).

[3] Atomic ratio of oxygen consumed and ammonia-N excreted (mean ± SD; GRL, $N = 7$; ARP, $N = 6$).

[4] Condition Index (Dry soft tissue wt (g) × 1000/dry shell wt (g), mean ± SD; GRL, $N = 6$; ARP, $N = 5$). NA = not applicable.

[5] C:N ratio ($\mu g/\mu g$, mean ± SD; ARP, $N = 6$; GRL, $N = 7$) of tissue samples.

[6] EC = energetic content (kJ g^{-1} organic mass; ARP, $N = 6$; GRL, $N = 7$) of tissue samples.

tridium senile from both GRL (Y = 5.138X + 0.429, ANOVA $P = 0.0001$, $N = 10$, $r^2 = 0.977$) and ARP (Y = 3.75X + 5.151, ANOVA $P = 0.0001$, $N = 13$, $r^2 = 0.804$). When the slopes were compared from the Ford-Walford plots, the results from the anemone transplant experiments showed no significant differences in growth rates of ARP and GRL controls (ANCOVA, $P > 0.05$). Because the slopes of the control anemones are statistically homogeneous, we can compare the y-intercepts, which were significantly different (ANCOVA, $P < 0.001$), indicating that the mean size of ARP control anemones was larger than that of the GRL control anemones (Fig. 4a). Anemones transplanted from GRL to ARP showed a significant increase in growth rates (ANCOVA, $P < 0.05$) compared to GRL controls (Fig. 4b), despite the low sample size ($N = 5$) for recovered transplants. Anemones transplanted from ARP to GRL showed no changes in growth rate compared to ARP controls (ANCOVA, $P > 0.05$), but a comparison of the y-intercepts again reveals a significant decrease in the mean size of ARP anemones transplanted to GRL (ANCOVA, $P < 0.001$) when compared to ARP controls (Fig. 4c).

Ford-Walford plots comparing changes in shell length for *Modiolus modiolus* for the two sites from 1989 to 1990 showed no significant differences between controls, or controls and transplanted mussels (ANCOVA, $P < 0.05$, data not shown), although the mean shell length of GRL control mussels was greater than that of ARP controls, mean shell length of mussels transplanted from ARP to GRL increased, and mussels transplanted from GRL to ARP actually decreased in shell length. The condition index for *M. modiolus* was significantly different

for ARP and GRL mussels, with GRL mussels showing higher values (Table III). This indicates that a larger proportion of assimilated energy was being allocated into somatic growth consistent with the absence of any significant difference in shell length. Using the 1990 data we subsequently compared the relationships between shell length and dry tissue weight for the control and transplanted mussels. The slope of mean tissue weight as a function of shell length was significantly higher in control mussels from GRL than in control mussels from ARP (ANCOVA, $P < 0.05$, Fig. 5a); whereas this slope, in mussels transplanted from GRL to ARP, was significantly lower (ANCOVA, $P < 0.05$) than that in the GRL controls (Fig. 5b), suggesting a loss of tissue mass during the period of transplantation. Conversely, ARP mussels transplanted to GRL showed a significant increase in mean tissue weight as a function of shell length, suggesting again that more energy was directed into tissue growth in these mussels—a result consistent with the condition indices from the respective populations (ANCOVA, $P < 0.05$, Fig. 5c).

Discussion

Although these measurements of food, flow, and SFG in *Metridium senile* and *Modiolus modiolus* represent but a snapshot in time, we note that Navarro (1990), in a two-year study, found similar results for *M. modiolus* in Newfoundland; *i.e.*, he showed positive SFG in June and negative SFG in August for all size classes of mussels studied (1.0, 2.0, and 5.0 g). Our August results differ from those of Navarro (1990), reflecting, perhaps, differences in seston

quality, and therefore energy content, or the quantity of seston at both of our sites, which was slightly higher than in Newfoundland. Seasonal decreases of SFG in other bivalve molluscs have been attributed to decreased seston concentrations (Griffiths and Griffiths, 1987), and intertidal bivalves usually show negative SFG as a result of the combined effects of decreased seston concentration and the tidally determined decrease in feeding time during the late summer (Griffiths and Griffiths, 1987). Our positive SFG results for August are not entirely unexpected because year-round positive SFG has been reported for blue mussels (*Mytilus edulis*) living in a subarctic environment with concentrations of particulate organic matter (Thompson, 1984) similar to the values reported in this study. Our conclusion that, for *Modiolus modiolus,* SFG is closely related to seston concentrations is also consistent with the different levels of productivity characteristically found at onshore and offshore sites. These differences in productivity are well known from successive years of oceanographic data collected in the Gulf of Maine (Townsend *et al.,* 1984; Townsend and Spinrad, 1986; Morrison and Townsend, 1988). Moreover, the more comprehensive work of Navarro (1990) is in agreement with our findings that total seston concentration is more important than seston flux in determining the SFG and biomass of horse mussels. Previous work on *Mytilus edulis* (Page and Ricard, 1990), in which secondary productivity of blue mussels was limited by offshore seston concentrations, also supports our conclusions.

The indirect measurements of growth on anemones and mussels, using an energetic approach, are corroborated by the direct measurements of growth from reciprocal transplants between the two study sites. The direct growth data show that, on average, anemones from ARP are larger than those from GRL, and that anemones transplanted from GRL to ARP grow faster. These data support the hypothesis that water flow, and thus the flux of seston, is important when considering the secondary productivity of these passive suspension feeders. Higher fluxes, however, do not always give positive results, as shown by the recent work of Eckman and Duggins (1993), in which benthic suspension feeders responded both positively and negatively as flow increased. For anemones, the flux of seston at each site appears to support different levels of secondary productivity, reflected in anemone numbers and biomass, at each site. Within each site, however, anemones maintain positive SFG into the summer, have similar biochemical compositions, and show tissue energy contents comparable to those of well-fed *Anthopleura elegantissima* (-23.4 kJ g^{-1} organic mass, Shick, 1991). It appears that, for these sites, flux of seston is an important variable regulating secondary productivity and physiological performance.

Significant differences in SFG between onshore and offshore mussels are not supported by the shell growth data, which are not significantly different between sites. The trend in mussel controls and transplants, however, suggests that shell growth may also be effected by differences in seston concentration. The mussel SFG data are supported by examining the changes in dry tissue weights in control and transplant mussels. Mussels have higher mean dry tissue weights at GRL, which has a higher concentration of seston. Moreover, mussels transplanted to GRL gain weight relative to ARP controls, and mussels transplanted to ARP lose weight. The most reasonable explanation for these changes is reflected in the SFG. The specific reasons for allocating more energy to somatic tissue growth than to shell growth are not discernible from this work; but the condition index we used provided another way of assessing the partitioning of energy in horse mussels from GRL (Table III). These growth data represent the integrated organismal response to environmental changes over a year-long period not included in this study. The use of scope for growth as an indicator of growth itself has been evaluated for the American oyster, *Crassostrea virginica* (Dame, 1972), and the blue mussel, *Mytilus edulis* (Bayne and Worrall, 1980). The two-year study by Bayne and Worrall (1980) revealed that physiological estimations of growth agreed well with direct measurements of tissue growth, as demonstrated in this study.

How are these physiological responses to differences in flow and seston availability reflected in the distribution and abundance of these benthic suspension feeders? Differences in population size distributions, due to changes in physical factors (*e.g.,* flow-induced biomechanical constraint on the size range of anemones), are probably of minor importance at these sites (Sebens, 1984, 1987; Shick *et al.,* 1979), but total numbers and biomass (= secondary production) for anemones and mussels in 1989 and 1990 are different, with anemone densities higher at ARP and mussel densities higher at GRL (Witman and Sebens, 1988; Witman, unpub.). We believe that this can be partially explained by the differential response demonstrated by anemones (passive suspension feeders) and mussels (active suspension feeders) to flow and seston concentration.

Flow regime alone, however, can influence the population structure of these animals by its effects on organismal performance. Flow-modulated rates of metabolism have been demonstrated in a number of marine organisms, including *M. senile,* that are dependent on direct gas exchange through their tissues (Patterson and Sebens, 1989; Patterson *et al.,* 1991; Lesser *et al.,* 1994), and certainly influence the rates of food capture by *Metridium senile,* a passive suspension feeder. Our results do not show any evidence of flow-modulated respiration rates in

A

B

C
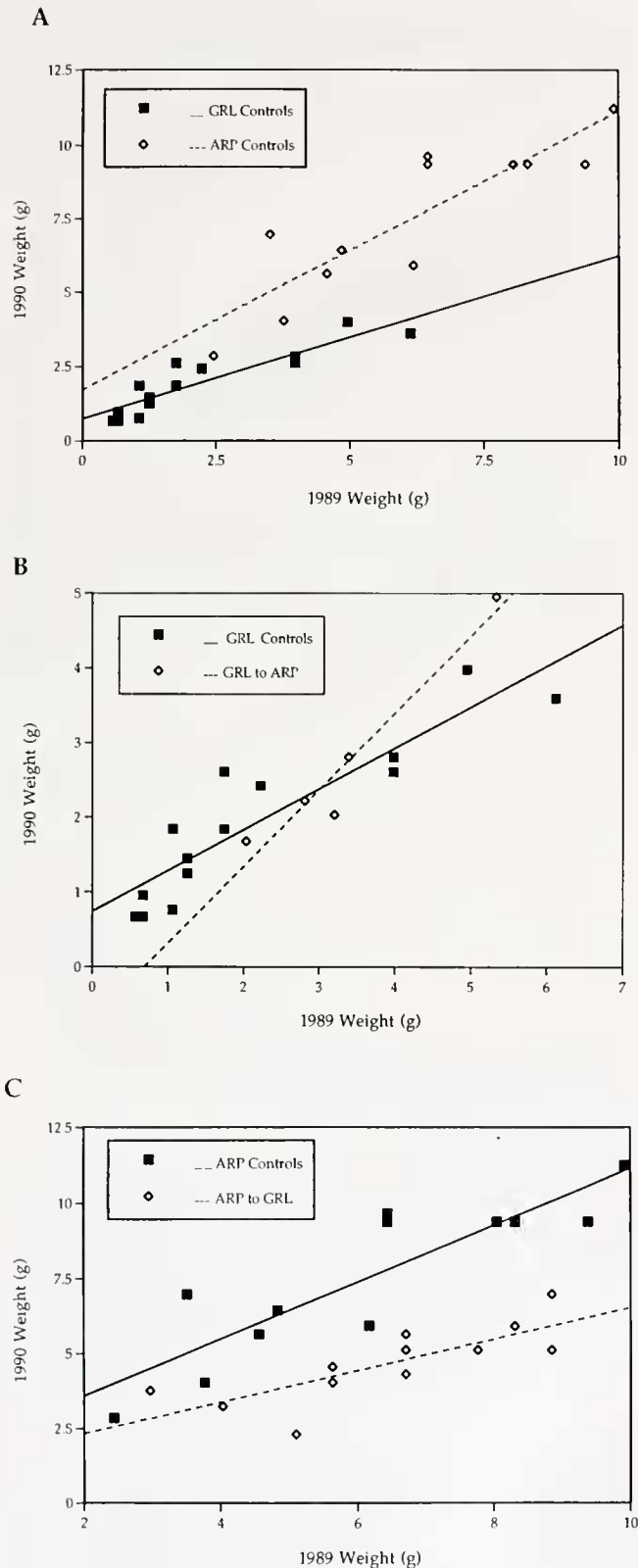
Figure 4. Results from the reciprocal transplant studies, Ford-Walford plots of 1989 and 1990 tissue dry weights. (A) *Metridium senile* caged controls; GRL = Monhegan Island, Gull Rock Ledge (Y = 0.481X + 0.84, N = 15, r^2 = 0.797, P < 0.001), ARP = Ammen Rock Pinnacle

M. senile (Fig. 2a). Higher growth efficiencies (K_2) in ARP anemones are the result, not only of higher consumption and assimilation, but also of the lower respiration rates observed in these anemones. The high flow regime at ARP would be expected to result in higher, flow-modulated metabolic rates (Patterson, 1992). Anemones reciprocally transplanted between ARP and GRL for one year exhibit an incomplete compensatory response, with respiration rates staying nearly the same as the control rates (Lesser, unpub.). This suggests either a genetic component constraining the phenotypic response of respiration rates between sites or an irreversible nongenetic adaptation (Zamer and Mangum, 1979). Anemones at ARP were found in large groups at high densities during the time of this study, and all of the field observations confirmed that anemones were fully expanded and not collapsing on the downstream side of the ambient flow. This could have been the result of the effects of neighbors on the flow regime or of the material properties of the anemones themselves. The issue of local selection of specific genotypes due to flow regime for low rates of respiration or enhanced materials properties remains to be assessed.

The effect of flow *per se,* or seston flux, on bivalve feeding and subsequent growth is poorly understood (Grizzle and Lutz, 1988). Within the range of flows measured at ARP and GRL at 30–35 m (Table 1) nonsiphonate bivalve molluscs generally show a negative effect of increasing water flow on filtration or clearance rate (Cahalan *et al.,* 1989; Wildish *et al.,* 1987; Grizzle *et al.,* 1992). Flow-induced inhibition of feeding cannot be ruled out for *M. modiolus* at ARP. In a recent study on *Mytilus edulis,* the blue mussel, a mytilid like *Modiolus modiolus,* the percent seston filtered decreased as flow increased up to 25 cm s^{-1}; flows greater than this did not further decrease feeding (Wildish and Miyares, 1990). Additionally, although the effect of food concentration on filtration rate in *M. modiolus* is not known for these particular populations, rates of filtration as a function of food concentration for this species (Winter, 1978) suggest that the concentrations of food measured at ARP and GRL are within the range in which maximum sustained rates of filtration would be expected without the production of pseudofeces.

For the sampling periods of this study, seston quality should not have been a determining factor: the POM concentration and seston C:N ratios indicate that the food source provided sufficient ingested ration with a low inorganic content for the mussels and anemones to be car-

(Y = 0.772X + 2.526, N = 13, r^2 = 0.618, P < 0.001). (B) *Metridium senile* transplants; GRL controls as above, GRL to ARP caged transplants (Y = 1.03X − 0.72, N = 5, r^2 = 0.938, P < 0.005). (C) *Metridium senile* transplants; ARP controls as above, ARP to GRL caged transplants (Y = 0.525X + 1.257, N = 14, r^2 = 0.62, P < 0.001).
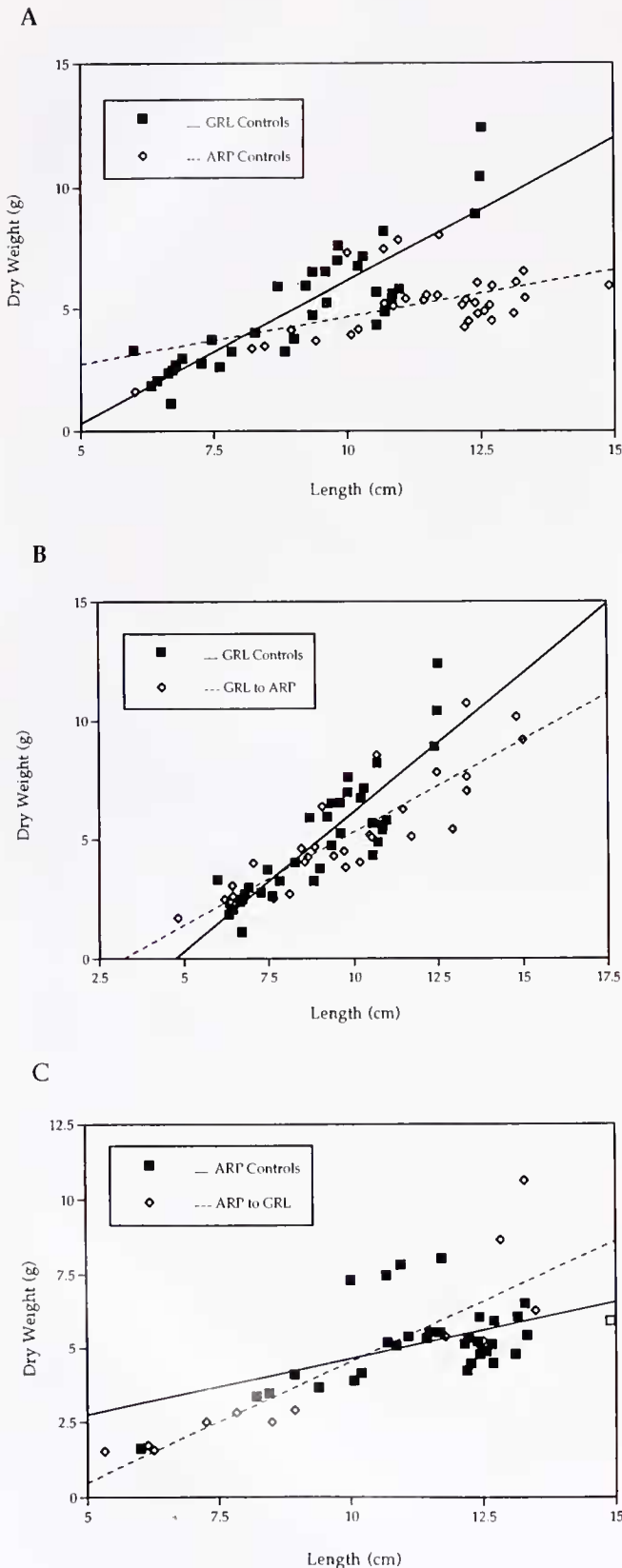
A

B

C

Figure 5. Results from the reciprocal transplant studies, allometric plots of 1990 shell lengths and 1990 dry somatic tissue. (A) *Modiolus*

bon and nitrogen replete (Russell-Hunter, 1970). The protein content of horse mussel tissue is highest during the spring and summer, varies from 65–75%, and is dependent on seston food quality—specifically, the protein content of the seston (Navarro, 1990). In our study, the mass fraction of protein for both ARP and GRL mussels in the summer ranged from 60 to 65%, and the seston quality was high as in the study by Navarro (1990). For our mussel samples, the C:N ratio of tissue was low and not significantly different at the two sites, suggesting that food quality (in terms of carbon and nitrogen) was not decreasing in either population. Also, the energetic content of the mussel tissues at both sites was equivalent, and was slightly higher than that of Newfoundland mussels (Navarro, 1990); these results are consistent with high energetic values for the seston.

Differences in time-averaged seasonal levels of pelagic productivity are important features of these sites. But on shorter time scales, localized oceanographic features, such as island mixing at Gull Rock Ledge (Townsend *et al.*, 1983) or internal waves in the central Gulf of Maine (Lande and Yentsch, 1988; La Violette *et al.*, 1990), may bring the particulate maximum layer down to the depth of these suspension-feeding communities (Witman *et al.*, 1993) or resuspend particulate food and benthic phytoplankton into the water column, thus maintaining a positive SFG in both spring and summer.

Furthermore, both locations are likely to be influenced by local kelp beds. Duggins *et al.* (1989) demonstrated that kelp-derived organic carbon can further enhance the secondary productivity of sea anemones and mussels in nearshore benthic communities where phytoplankton production alone was believed to be limiting. These localized features may be important in maintaining a positive SFG over longer periods, but do not obscure the effects of regional differences in productivity.

Intertidal invertebrates exhibit compensatory responses to the decrease in food or energy arising from emersion and the resulting changes in temperature, gas exchange, metabolism, and duration of feeding (Newell, 1980; Shick *et al.*, 1988; Shick, 1991). The interspecific variation in these responses to a changing environment is correlated with the distribution and abundance of these sessile intertidal assemblages. Similar comprehensive work on the physiology of subtidal suspension-feeding invertebrates

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modiolus caged controls; GRL = Monhegan Island, Gull Rock Ledge ($Y = 1.13X - 5.226$, $N = 36$, $r^2 = 0.747$, $P < 0.001$), ARP = Ammen Rock Pinnacle ($Y = 0.377X + 0.875$, $N = 34$, $r^2 = 0.257$, $P < 0.005$). (B) *Modiolus modiolus* transplants; GRL controls as above, GRL to ARP caged transplants ($Y = 0.767X - 2.439$, $N = 31$, $r^2 = 0.765$, $P < 0.001$). (C) *Modiolus modiolus* transplants; ARP controls as above, ARP to GRL caged transplants ($Y = 0.814X - 3.592$, $N = 15$, $r^2 = 0.775$, $P < 0.001$).

under changing environmental conditions is lacking, except for scleractinian corals (Muscatine, 1990). We propose that for the suspension feeders examined in this study, their physiological ecology and differences in functional responses to flow and food availability are important features influencing their distribution and abundance.

Acknowledgments

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